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REGULAR ARTICLE

Grassland cutting regimes affect soil properties, and consequently vegetation composition and belowground plant traits

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Abstract
Background and aims Machine mowing, mimicking the traditional hand mowing, is often used as a successful management tool to maintain grassland biodiversity, but few studies have investigated the long-term effects of traditional versus mechanical mowing of plant communities. Machine mowing as opposed to hand mowing causes soil compaction and reduction of soil aeration. In response, we expected strong effects on below-ground plant traits: root aerenchyma formation and superficial root growth, and no specific effects on aboveground traits. Effects were expected to be more pronounced in soils vulnerable to compaction.
Methods We evaluated the changes in above- and belowground plant traits in a long-term (38-year) experiment with annual hand-mowing and machine-mowing management regimes on two different soil types: a coarse structured sandy soil and a finer structured sandy-organic soil
Results Only on the organic soil, long-term machine mowing leads to lower soil aeration (more compacted soil) and a marked change in the belowground trait

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distribution of the plant community. Here we find a higher cover of superficially rooting species and marginally significant lower cover of species without morphological adaptations to soil hypoxia, but no effect on species with a high capacity of forming aerenchyma.
Conclusion Mowing with heavy machines on soils vulnerable to compaction affect the vegetation according to changes in soil physical conditions. This is reflected in a shift towards communities with greater proportion of superficially rooting species. Our results illustrate the sensitivity of grasslands to slight changes in the management regime.

Keywords Mowing · Soil redox potential · Aerenchyma · Rooting depth · Aboveground traits · Long-term experiment

Introduction

The structural changes in agriculture, i.e. the intensification of agriculture and the abandonment of marginally productive farmland (Bignal and McCracken 1996; Henle et al. 2008), lead to a remarkable loss of semi-natural grasslands in Western Europe (e.g. Hooftman and Bullock 2012; Dierschke and Wittig 1991; Fuller 1987; Wallin et al. 2009). In an effort to maintain or restore valuable grassland plant communities that are of nature conservation interest, management regimes are often established. The most commonly used management practices are cessation of artificial fertilizer application and subsequent cutting and/or grazing , which have shown to be effective measures for maintaining or restoring species-rich grassland communities (Walker et al. 2004).

In contrast to traditional practices, cutting in these grasslands is often done with heavy machinery, as traditional hand cutting is costly (Liira et al. 2009). Although a number of studies have evaluated differential effects of these management regimes on aboveground plant traits (Huhta et al. 2001; Liira et al. 2009), to our knowledge no studies have shown effects of different cutting regimes on belowground plant traits. We argue that these effects are likely, but will depend on the soil type. From agricultural practices it is known that wheel traffic from heavy agricultural machines has a strong soil compacting effect (Hamza and Anderson 2005), which is not expected as a result of hand mowing. Soil physical properties, such as soil moisture, soil aeration and denitrification, can be strongly affected by soil compaction (Soane et al. 1982; Jensen et al. 1996; Nevens and Reheul 2003), especially in wet soils with a high organic fraction or soils with fine texture (Rasiah and Kay 1998). Strong negative effects of soil compaction on plant performance are frequently observed when soils are wet during compaction (Voorhees et al. 1985; Nevens and Reheul 2003). This happens because of two reasons. Firstly, root growth may be physically impeded by soil density (Engelaar et al. 1993; Striker et al. 2007) and secondly, compaction increases the chance of oxygen-deficient conditions because of smaller pore size and increased water content (Vartapetian and Jackson 1997; Jackson and Armstrong 1999). Under dry conditions soil compaction may even be favourable to plant performance, as compaction may increase mesoporosity and soil hydraulic conductivity and thus improves access to water and nutrients (Voorhees et al. 1985).

When managed with heavy machines, compaction can be expected to act on plant community composition, especially if soils are sensitive to soil compaction. If soil compaction leads to hypoxia in the rooting zone, aerenchyma formation in roots and species with superficial rooting can be expected (Vartapetian and Jackson 1997; Elzenga and van Veen 2010) and species that are unable to produce such adaptations may be selected against. However, species with aerenchyma in strongly compacted soil may also have a disadvantage due to reduced physical strength of these roots (Engelaar et al. 1993; Striker et al. 2007). So, while machine mowing and hand mowing have similar aboveground effects in terms of reducing light competition, belowground responses to the different management regimes may be strongly differing.

In this study, we evaluated a long-term (38 year) experiment in which a machine-cutting regime and a hand-cutting regime were installed on two previously similar sites. The first research field was located on a sandy soil with a relatively high content of very fine organic matter (38.5–47 %) resulting in a cemented soil structure, thus leading to lower soil hydraulic conductivity and higher water holding capacity (hereafter: organic soil). The second research field was located on an adjacent field with sandy soil with less organic matter (11.6–13.2 %) and thus a coarser

single-grained structure and lower water holding capacity (hereafter: sandy soil).

Firstly, we expected a divergence in vegetation development and species composition as well as abundance between the machine mown and hand mown treatments. We were interested to know to which extent these differences in vegetation were related to plant traits. We expected differences in the root traits, i.e. an increase in cover and number of species with aerenchyma formation or superficial root growth in the machine mown treatment. Furthermore, we expected that differences between machine mown and hand mown treatments are stronger on an organic soil than on a sandy soil. In contrast to belowground traits, aboveground traits are not directly affected by changing soil physical properties. Thus, we had no a priori expectations on treatment effects on canopy height, specific leaf area, and leaf dry matter content.

Methods

Study site and treatments

The study site Loefvledder (53°05′N, 6°40′E) is located in the brook valley of the Drentsche Aa, The Netherlands. It is in the upper course of the brook valley at 7 m above Dutch Ordnance Level, and is characterized by a sandy subsoil. The study site includes two fields with different agricultural history before they were transformed into a nature reserve. The first field (organic soil) was acquired in 1967 ('old field' in Bakker et al. (2002)), and fertilizer application was stopped in the same year. The vegetation harboured species of both nutrient-rich (*Festuca rubra, Ranunculus repens*, *Rumex acetosa*, *Trifolium repens*), and intermediate (*Agrostis capillaris, Anthoxanthum odoratum*, *Juncus effusus*) soil conditions (Ellenberg et al. 1992). After 10 years, species of nutrient-poor soil conditions occurred in both treatments (*Carex nigra*, *Juncus conglomeratus* and *Viola palustris*), and *Festuca rubra* especially in the hand mown treatment, whereas *Agrostis canina* and *Juncus effusus* characterized the machine mown treatment (Bakker 1989). The mowing regime resulted in a decline of yield of about 400 to 650 g/m^2 in the 1970s to 250 to 350 g/m^2 in the 1980s in both mowing treatments (Bakker 1989). The other field (sandy soil) was acquired in 1972 ('new field' in Bakker et al. (2002)) and fertilizer application stopped in that year. The vegetation included many species of nutrient-rich soil conditions (*Agrostis stolonifera*, *Lolium perenne*, *Poa pratensis*, *Poa trivialis*), and few species of intermediate soil conditions (*Holcus lanatus*, *Festuca pratensis*) (Bakker 1989). After 10 years species of nutrient-rich and high moisture soils occurred in both treatments (*Cardamine pratensis*, *Cerastium fontanum*, *Ranuculus repens*, *Rumex acetosa*). Moreover, *Cirsium arvense*, *Festuca rubra* and *Potentilla anserina* occurred in the hand-mown treatment, and *Agrostis stolonifera* and *Poa trivialis* in the machine-mown treatment. In the latter regime, however, also *Agrostis capillaris* and *Rhinanthus angustifolius* of intermediate soil conditions were found (Bakker 1989). The mowing regime resulted in a decline of the yield of about 600 to 900 g/m^2 in the 1970s to 200 to 500 g/m^2 recently in both mowing treatments (Bakker et al. 2002). At the start of the experiment, both fields had a similar groundwater level of 56.3 cm ± SD 16.1 cm for the organic soil and 58.7±SD 23.9 for the sandy soil (yearly average) below ground level. We used data from two mowing experiments in each field. Hence, both experiments were carried out within a single field with the same agricultural history and soil type. The experiments started in 1972, after which the vegetation was mown once every year in July by means of machines in one treatment and by hand using a petrol scythe in the other treatment. Hay was removed with machines in the machine mown treatment and raked by hand in the hand mown treatment. The machines that were used in this treatment were comparable to those used in conventional agriculture and weighed between 6 Mg, which equals a stress on the soil between 100 kPa and 160 kPa (Hamza and Anderson 2005). Hence, on both mowing treatments aboveground biomass was removed. As this resulted in similar amounts of standing crop (Bakker 1989; Bakker et al. 2002), competition for light did not differ between treatments. More details on the setup of the field experiment can be found in Bakker (1989).

Each treatment included six permanent plots of 2 m x 2 m. Dynamics of the species composition of the plant communities were recorded in most years between 1972 and 2010 by estimating cover of individual species according to the decimal scale (Londo 1976). A total of 75 species were recorded on the two fields over the years. The unique long-term character of the experiment is necessary to reveal long-standing effects on

community development of vascular plants. Unfortunately the low sample size is the downside of this. The vegetation diverged in both mowing treatments already after 10 years (Bakker 1989) in both fields. Hence, the set-up of the experiment offers the unique possibility to compare the vegetation composition after 38 years of continuous mowing treatment on different soil types, and to relate it to plant traits.

Measurements on soil physical properties

Two different methods were used for determining soil compaction. With the first method, bulk density was determined near each permanent plot by taking the average of two soil samples. Soil samples were taken in July 2010 using a Tullgren soil core device with a diameter of 10 cm, which is often used to sample soil fauna (Van Straalen and Rijninks 1982) and minimizes soil compaction while taking the core. From these cores, living aboveground vegetation was carefully cut and removed before the soil sample was taken. The samples were weighed, dried (70 °C, 48 h) and weighed again to determine bulk density. With the second method, we determined a proxy for the air filled porosity , using an approach that was first described by Jafarzadeh (2006) and which is based on 'dynamic compaction'. According to this method, the volume of soil on which a weight is dropped decreases asymptotically with the number of times that a weight is dropped on the soil, until all air is pushed out. Maximal compaction is typically reached after dropping the weight ten times (Jafarzadeh 2006). These samples were taken pairwise with the other soil samples using the same soil corer as described above. We used a 1.5 m long PVC cylinder (Ø 10 cm) to compact a 15 cm high soil core with equal diameter, which was placed at one end of the PVC cylinder. A lid was put on the bottom of the PVC cylinder, in order to avoid loss of sample. From the top of the vertically placed cylinder, we applied a force of 6.5 kN m^{-2} by dropping a weight of 5 kg, ten times. As a measure for the total amount of air-filled porosity, we measured the decrease in volume of the sample. As penetrometer readings are known to be sensitive to differences in density of plant roots, differences in texture and differences in soil moisture (Gerrard 1982; Borchert and Graf 1988), we preferred the two methods described above in this study.

As a proxy for the oxygen level in the soil we measured the soil redox potential. We chose a set up in which four electrodes with a platinum tip and one Ag/AgCl reference electrode (Cole-Palmer®) were connected to a Graphtec GL200 Datalogger (Graphtec GB Ltd). All measurements were taken at the 23rd of June 2011. In order to obtain a depth-profile of the soil redox potential, all electrodes were placed into the soil first at 5 cm and subsequently at 10 cm depth. Measurements were read out exactly 2 min after the electrodes were placed at a certain depth. Readings were corrected for the potential of the reference electrode (+197 mV) and pH. Averages of the four platinum electrodes were used for further analyses. Quick in situ measurements on redox potential may not necessarily reflect absolute values and are highly variable throughout the year, but are suitable for making comparisons between treatments (van Bochove et al. 2002).

Belowground traits

To study the potential impact of soil compaction on species composition in the studied grasslands, we evaluated species belowground traits and species aboveground traits. We used the ability to produce aerenchyma and maximal rooting depth as species belowground traits. According to these two characteristics, species were assigned to three groups: species with a maximal rooting depth less than 10 cm were assigned to group 1. Species with less than 15 % aerenchyma and rooting depth deeper than 10 cm were assigned to Group 2. Species with the ability to produce more than 15 % aerenchyma and rooting depth more than 10 cm were assigned to Group 3. As previous analyses have shown that the threshold for the minimum amount of aerenchyma (porosity) that is functionally significant in oxygen-deficient soil can also be defined as 10 % (De Willigen and Van Noordwijk 1989), we reran the analyses on aerenchyma with a threshold between group 2 and 3 at 10 % aerenchyma. All frequent species (species with cover >5 % in any year or occurring for at least five consecutive years in a plot) at the research locations were assigned to one of the groups. Values for maximal rooting depth where taken from literature (von Kutschera et al. 1982) and values for aerenchyma (root porosity) were either taken from literature (von Kutschera et al. 1982; Justin and Armstrong 1987) or were determined from plants grown on hydroculture. Root trait data was available for 46 of the 75 species from the total species covering the most frequent and abundant species. For details on

species root traits and species division into groups as well as species averaged abundance data, see electronic appendix, table 1.

All species in which we experimentally determined root porosity were taken from the Drentsche Aa research location. Three specimens for every species were taken on the 9th of August 2010. Every specimen was carefully rinsed and placed on hydroculture (electronic appendix, Fig. 1). Plants were grown at 0.25 strength Hoagland-solution (Hoagland and Arnon 1950). After 2 weeks, all plants were put in a bath of 0.05 % agar in nutrient solution (w:v) to minimize oxygen diffusion in the water column, hereby mimicking a hypoxic environment (Wiengweera et al. 1997). Acidity of the solution was kept constant at pH6 (± 0.2) and the hydroculture medium was replaced biweekly to avoid algal growth. After another 4 weeks, plants were harvested. From every individual, five 1 cm root segments were carefully cut from the adventitious roots, 2 cm from the root tip. As a proxy for porosity, we used the percentual volume of air inside the aerenchyma of these root segments (Visser and Bogemann 2003). The air-filled aerenchyma in the submerged root particles was filled with water using a vacuum pump (Emergo BV, Landsmeer, the Netherlands) by applying a vacuum of 0.04 Bar for 5 min, which was repeated three times. To calculate the increase in water in the pores, weight increase of root particles was determined by weighing before and after the aerenchyma was infiltrated. As a species-specific proxy for porosity, we used the average of all individuals of one species.

Aboveground traits

We used specific leaf area (SLA), leaf dry matter content (LDMC) and canopy height (CH) as species aboveground traits. For details on species traits, see electronic appendix, table 2. All three traits are commonly used to indicate responses to a multitude of changes in environmental circumstances as they contribute information on interspecific variation (Wilson et al. 1999; Westoby and Wright 2006). Specific leaf area correlates with photosynthetic capacity and leaf lifespan (Ryser and Urbas 2000; Wright et al. 2004; Shipley 2006). Leaf dry matter content is associated with leaf lifespan (Weiher et al. 1999; Ryser and Urbas 2000) and community litter decomposition rates (Quested et al. 2007; Laughlin et al. 2010). Canopy height is a good proxy for the competitive vigour of a species (Gaudet and Keddy 1988; Tilman 1988). For most of the species we used trait data from own measurements on individuals sampled in the surroundings of the study site. The values of 26 missing species were taken from the trait database LEDA (Kleyer et al. 2008). After replenishing our own trait data with data from LEDA aboveground trait data was available for most of the 75 species observed over the years (CH: 70, SLA: 68, LDMC: 67).

Our own aboveground trait measurements followed the standard protocols of the LEDA-trait base (Knevel et al. 2003). We measured canopy height from the base of the plant to the highest photosynthetic tissue in metres. Sampled leaves were scanned with the HP Image & Scanning Program (2009) and afterwards leaf fresh weight was determined. After drying in the oven at 70° C for 24 h finally leaf dry weight was determined. Leaf area (mm^2) was determined analysing the leaf scans in the software Lafore (Lehsten 2005). Leaf dry matter content was calculated as the ratio of dry to fresh leaf weight ($mg\,g^{-1}$) and specific leaf area was calculated by dividing the area of the fresh leaf by the dry weight ($mm^2\,mg^{-1}$). In the field sampled plant material was cooled and transported between moist paper sheets in self-sealing plastic bags and after sorting and cleaning in the lab at the same day stored in a freezer at −18° C. This method of freezing allows large numbers of samples to be taken during the summer and to be analysed later on in the year. This method was applied successfully for the Northwest-European trait database, LEDA (Knevel et al. 2003). Fragile leaves were processed immediately after sampling.

Ellenberg-values

According to our hypothesis, the soil compacting machine mown treatments should result in lower soil aeration and higher soil moisture, to which species with adaptations to high levels of soil moisture should respond positively. This reaction is expected to be captured in the Ellenberg-moisture values for these species (Ellenberg et al. 1992). Therefore, we performed an analysis on the weighted community average of the Ellenberg moisture values. We used cover-weighted community Ellenberg indicator values for nitrogen to show the trend in nutrient availability over time (Ellenberg et al. 1992).

Data analysis & statistical analysis

To evaluate the two mowing treatments and whether the treatment effect was different in the two fields, we used a paired t-test on the soil data, a Bray-Curtis dissimilarity index on the floristic data and mixed models on community trait data.

We calculated the floristic similarity between the two treatments (hand mown and machine mown) for every time step, to compare the floristic composition between treatments within years. In order to calculate Bray-Curtis floristic dissimilarity index between treatments within fields, plant species cover data of every permanent plot in a given treatment and field was compared to cover data for all plots in the other treatment of the same field. These 6^6 comparisons were used as the dissimilarity between treatments in a given year and field. Under the assumption that treatment differences do not lead to a divergence in the floristic composition, the dissimilarity index should only show a non-directional fluctuation. Differences between fields were tested using mixed models (Model structure: lmer(y.bray.cover ~ x.field * x.year + (year|plot)), for more details see below). We calculated the Bray-Curtis dissimilarity index using R (RDCT 2008) with package 'vegan' (Oksanen et al. 2008).

We applied mixed models to test for differences between treatments in community belowground traits, community aboveground traits and community Ellenberg moisture values, both weighted and unweight by cover. Analysis were done in R (RDCT 2008) with package 'lme4' (Bates et al. 2011) to calculate models and package 'languageR' (Baayen 2011) to calculate *p*-values. The mixed models were structured as follows:

$$\mathrm{lmer}([y]^{\sim}\mathrm{x.year}^{*}\mathrm{x.treat}^{*}\mathrm{x.field} + (\mathrm{year}|\mathrm{plot})).$$

The year of recording (x.year), the treatment (x.treat) and the field (x.field) (main effects) and all their interactions were implemented as fixed effects and year in plot as random effects. For longitudinal data as in our case, where repeated measurements are taken on the same units over time, a random intercept and slope model with time (year) nested in subject (plot) is suitable (Bates 2011). The treatment effect in the models was evaluated by focusing on the resulting year-treatment interaction effect (detecting a treatment effect independent of the soil type) as well as the year-treatment-field interaction effect (detecting a treatment effect dependent on the soil type).

The community belowground trait used as dependent variables in the models, were calculated by respectively, using species presence-absence data (counting the species) and species abundance data (summing species' cover) per plot and year from the same root group. Both, species presence and species abundance reveal information on the constraining habitat filters. The dependent variables entered the model square root transformed, because of heteroscedascity (see Gotelli and Ellison 2004). For the aboveground traits: specific leaf area (SLA), leaf dry matter content (LDMC) and canopy height (CH), we used log transformed cover weighted and unweighted community means as dependent variable.

For the analysis of the Ellenberg values, we used the same mixed model structure as for the plant traits, but with community Ellenberg moisture values as response variable. We used cover-weighted community Ellenberg indicator values for nitrogen to show the trend in nutrient availability over time (Ellenberg et al. 1992). For the analysis on species diversity, we also used the same mixed model structure as for the plant traits, but with species numbers per plots and year as response variable. The variable year entered the mixed model on species diversity log transformed, as the changes in diversity mainly happened in the beginning of the experiment.

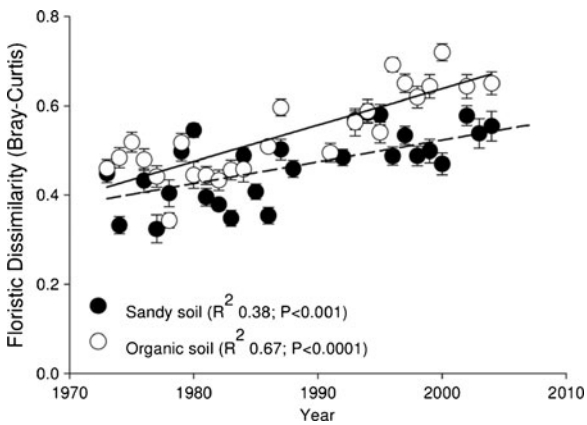

Fig. 1 Floristic dissimilarity ± SE between treatments on sandy soil (*filled circles*) and on organic soil (*open circles*). Organic soil: R^2 0.67; $P<0.001$; Sandy soil: R^2 0.38; $P<0.001$. Mean values are given ± SE

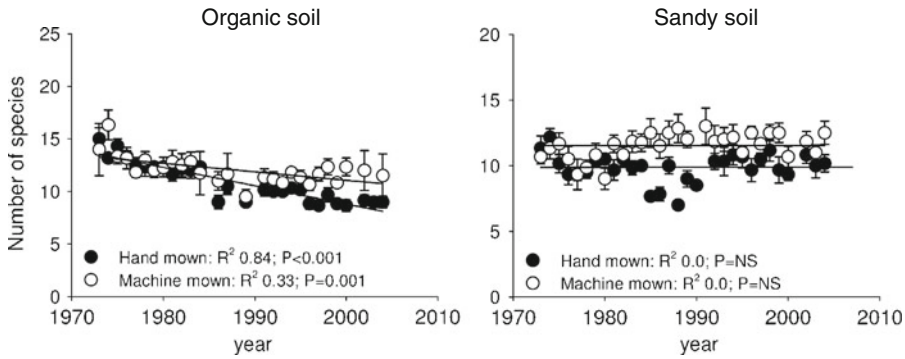

Fig. 2 Changes in total plant species numbers (averages of six plots of 2×2 m) per treatment over time. **a** denotes plant species numbers on sandy soil. **b** denotes species numbers on organic soil. Open symbols indicate machine mown treatments, closed symbols indicate hand mown treatments. Negative exponential fits depict the trend over time, for illustration purposes only

Results

We found divergent succession between treatments on both soils (main effect year: 0.007±0.0005, t=13.1, p<0.001). Species composition became more dissimilar over time on the organic soil than on the sandy soil, but this effect was only marginally significant (treatment-field interaction term (organic soil): 0.002± 0.001, $t_{(5,1)}$=1.8, p=0.065; Fig. 1). For a similar analysis on the Bray-Curtis dissimilarity on presence-absence, the increase in dissimilarity over time was less pronounced (main effect year: 0.001±0.0005, t=2.4, p< 0.05) and no difference between sites could be detected. So the effect of a growing dissimilarity was mainly represented in the relative abundances of the different species. Between 1973 and 2002, characteristic species from root group 1 show a much stronger increase in cover of plots on organic soil where they were found in the machine-mown treatment than in the hand mown treatment (Machine mown vs Hand mown between 1973 and 2002: *Hydrocotyle vulgaris* 66 % → 83 % vs 50 % → 33 %; *Potentilla erecta* 0 % → 100 % vs 0 % → 83 %; *Viola palustris* 0 %→ 100 % vs 0 % → 0 %; *Galium saxatile:* 33 % → 100 % vs 33 % → 0 %). The number of plant species showed a gradual decline on the organic soil, for both the hand mown as well as for the machine mown treatment (year-field interaction term (organic soil): −1.873±0.436, t=−4.3, p<0.001, Fig. 2a). On the sandy soil, no decrease in species richness was noted (Fig. 2b). Comparing the species diversity

Table 1 Soil physical properties in all treatments after 38 years. A paired t-test was done to identify significant differences. Mean values are given±SE. NS Not Significant, * P <0.05, ** P<0.01, ***P<0.001

	Machine mown	Hand mown	N	$F_{(df)}$	P
Organic soil					
Bulk density (gcm^{-3} dry weight volume)	0.42±0.05	0.41±0.03	6	$4.22_{(2,13)}$	NS
Air filled porosity (%; v:v)	11.0±0.84	21.3±1.14	8	$61.0_{(1,14)}$	***
Soil moisture content (gcm^{-3} dry weight volume)	0.74±0.02	0.67±0.02	6	$6.67_{(2,13)}$	*
Soil redox potential (mV) 5 cm	322.5±18.6	431.2±18.3	5	$21.7_{(1,8)}$	***
Soil redox potential (mV) 10 cm	271.4±41.2	416.1±20.5	5	$12.9_{(1,8)}$	**
Sandy soil					
Bulk density (gcm^{-3} dry weight volume)	0.67±0.05	0.68±0.05	6	$0.48_{(2,13)}$	NS
Air filled porosity (%; v:v)	17.7±0.69	23.2±0.68	8	$35.8_{(1,14)}$	***
Soil moisture content (gcm^{-3} dry weight volume)	0.60±0.02	0.60±0.03	6	$0.78_{(2,13)}$	NS
Soil Redox Potential (mV) 5 cm	429.8±7.9	455.2±12.3	5	$3.78_{(1,8)}$	NS
Soil Redox Potential (mV) 10 cm	410.3±11.0	451.6±20.0	5	$4.09_{(1,8)}$	NS

between treatments, machine mown plots lost fewer species over time (year-treatment interaction term: 1.22±0.436, t=2.8, p<0.01).

Effects on soil properties

We found a significantly more compacted, less porous soil in the machine mown treatment on both soil types (Table 1). However, compaction on the organic soil had a much stronger effect on soil physical properties than on the sandy soil. These differences were not observed in bulk density, possibly due to differences in root volume (Table 1). Soil redox potentials were significantly lower in the machine mown treatment on the organic soil, indicating lower oxygen availability (Table 1), but this effect was not found on the sandy soil. Mixed models on community Ellenberg moisture values show a significant year-treatment-field interaction effect on the organic soil, with higher Ellenberg moisture values in the machine mown treatment (Table 2, Fig. 3a). No year effect or treatment-year interaction effect was found on Ellenberg moisture values on sandy soil (Table 2; Fig. 3b).

Effects on belowground traits

In addition to the results on root traits, we found higher root volumes in the upper 10 cm of the organic soil in response to machine mowing (56.6 cm^3l^{-1} for machine mowing vs 11.5 $ml l^{-1}$ for hand mowing; t-test: $F_{(5,1)}$=5.4, P<0.001), but no such differences between treatments were found in the sandy soil (10.3 cm^3l^{-1} for machine mowing vs 3.1 cm^3l^{-1} for hand mowing; P=NS; Table 1). Functional belowground traits showed predominantly divergence between the treatments in organic soil (Fig. 4a–c), while we found no divergence between treatments on sandy soil (Fig. 4d–f). This is in agreement with the changes in soil properties and the increasing floristic dissimilarity between treatments on the organic soil. Species with superficial root growth (group 1) showed a significantly stronger increase in response to the machine mown treatment (Table 2, Fig. 4a). Then again, species with minor or no root adaptations (group 2) showed a significantly stronger decrease in cover in the machine mown treatment (Table 2, Fig. 4b). A steady increase in cover of aerenchyma-

Table 2 Different effects on aboveground and belowground traits as a result of compacting and non-compacting mowing treatments on the fine and sandy soil. CV: calculated using plant species cover, P/A: calculated using presence/absence of plant species in the plots. Estimates show effect of field (organic soil) and treatment (machine mown). The t-value is the ratio between estimate and standard error. NS: not significant; * p<0.05; ** p<0.01, *** p<0.005

Factor			Year main effect			Year-treatment interaction effect			Year-treatment-field interaction effect		
			Estimate ± SE	t-value	p	Estimate ± SE	t-value	p	Estimate ± SE	t-value	p
Aboveground traits	Specific leaf area (SLA)	CV	−0.004±0.002	t=−2.3	*			NS	0.008±0.004	t=2.0	*
		P/A	−0.005±0.001	t=−4.9	***			NS			NS
	Canopy height (CH)	CV			NS	−0.006±0.003	t=−2.1	*			NS
		P/A			NS			NS			NS
	Leaf Dry Matter Content (LDMC)	CV						NS			NS
		P/A	0.002±0.001	t=2.2	*			NS			NS
Belowground traits	Gr. 1 Super-ficial (<10 cm) rooters	CV			NS			NS	0.07±0.03	t=2.1	*
		P/A	−0.015±0.007	t=−2.1	*			NS	0.034±0.014	t=2.4	*
	Gr. 2>10 cm roots, <15 % aerenchyma	CV			NS			NS			NS
		P/A			NS	0.01±0.005	t=2.3	*	−0.017±0.007	t=−2.5	*
	Gr. 3>10 cm roots, >15 % aerenchyma.	CV			NS			NS			NS
		P/A			NS			NS			NS
Ellenberg indicator values	Ellenberg Moisture Value	CV			NS			NS	0.025±0.011	t=2.32	**
		P/A	0.018±0.005	t=3.99	**			NS			NS

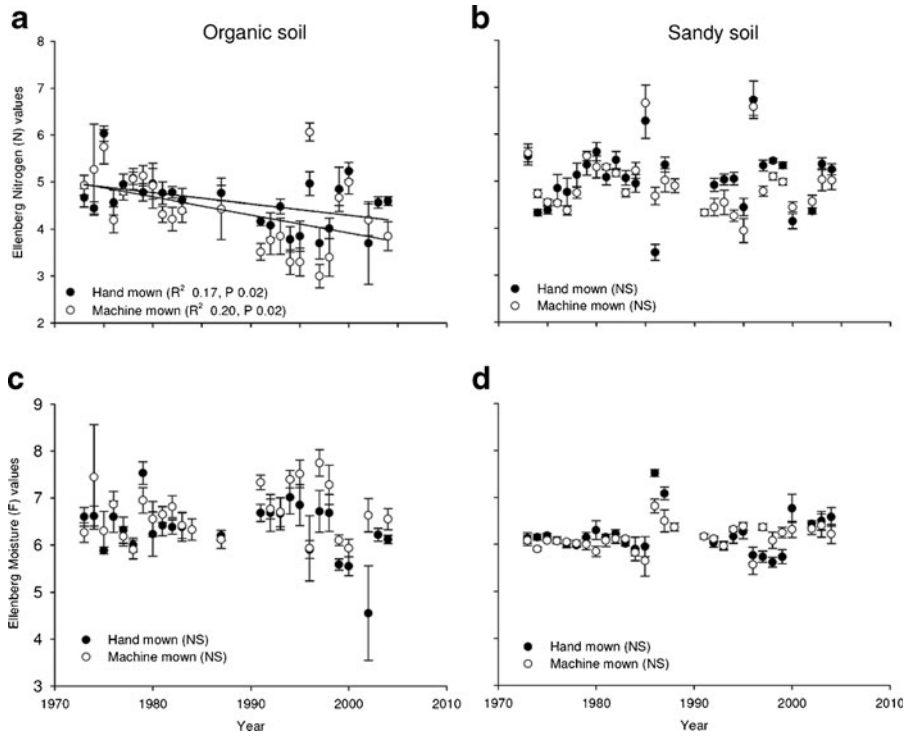

Fig. 3 Community weighted means for Ellenberg (N) nitrogen (**a**,**b**) and Ellenberg (F) moisture values (**c**, **d**). Closed symbols indicate hand mown treatments, open symbols indicate machine mown treatments. Linear fits are shown when significant or if interaction effect between treatments was significant, R^2 and P are given in figure legend. Fits depict the linear trend over time for illustration purposes only

forming species was observed in the organic soil (Fig. 4c), but we found no significant treatment-effect (Table 2). This indicates that the increase in the cover of aerenchyma-forming species occurred regardless of mowing regime. For none of the root groups on sandy soil, we found a significant difference

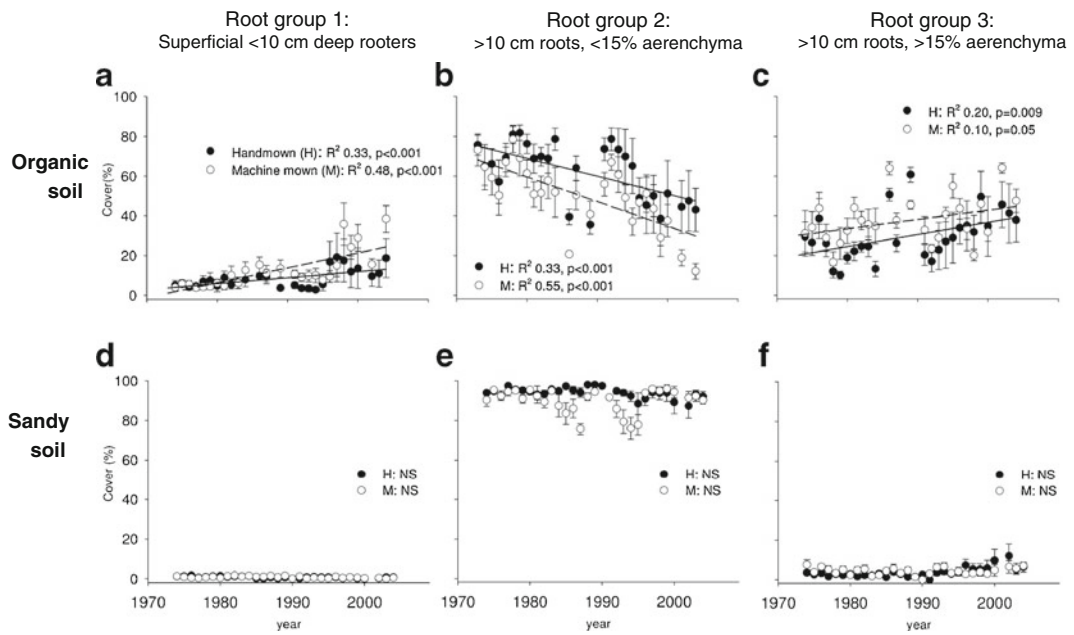

Fig. 4 Response of the three categories of plant rooting strategies in different long-term mowing regimes on organic (**a-c**) and sandy soil (**d-f**). Significant sfits for the different root groups and treatments are depicted $\alpha<0.05$. Mean values are given ± SE. Fits depict the linear trend over time for illustration purposes only

between treatments over time (Table 2). In addition to the absence of a year-treatment-field interaction effect on the sandy soil, we also could not detect any trend over time (Fig. 4d–f). A reanalysis excluding the outlier data from the years 1973, 1986 and 1989 lead to the same results.

Effects on aboveground traits

Of all aboveground traits, we found that the weighted community mean for canopy height reacted strongest to our treatment. Values are clearly lower in the machine mown treatment on both soils (Table 2). The community leaf traits (SLA and LDMC) showed a far less, and less consistent, divergence between treatments over time. The weighted community mean for SLA differed between treatments on organic soil and the weighted community mean for LDMC differed between treatments on sandy soil (Table 2). A re-analysis performed on presence/absence data for all plant species showed an even stronger effect of treatment on the community mean for canopy height, but no difference between the two soil types (Table 2). Using presence/absence data we also found no treatment effect on the community means for SLA and LDMC (Table 2).

Discussion

Our results show that long-term machine mowing leads to soil compaction and lower soil aeration, but mainly on an organic soil. This is reflected in a treatment effect on plant species composition and in a treatment effect on some belowground plant traits. Our results thus suggest that differences in root response to mowing treatments are highly related to abiotic soil conditions.

The effect of regular machine mowing

It is generally accepted that mowing with heavy machines leads to compacted soils (Soane et al. 1982; Hamza and Anderson 2005). We could detect these effects in both organic and sandy soil. Especially soils with a fine pore structure are vulnerable to compaction with heavy machines (Voorhees et al. 1985). A greater proportion of pores become water-filled and as a result, oxygen diffusion into the soil decreases. Our results on air-filled porosity and soil moisture show that soil aeration was significantly reduced in the machine mown organic soil. Consequently, we find a lower soil redox potential in the high-organic soil in response to machine mowing. These changes in the soil physical properties may have consequences for the growing conditions for plants. In waterlogged soils plant roots face oxygen shortage, which leads to reduced root performance and nutrient uptake (Colmer 2003; Bailey-Serres and Voesenek 2008). Prolonged negative effects of oxygen shortage can be mitigated by plants in several ways of which aerenchyma formation and superficial root growth are the most prominent (Armstrong et al. 1991). At shallower soil depth, we found that soil had a higher redox potential, indicating that superficial root growth may be beneficial to plant species that are less tolerant to soil hypoxia (Armstrong et al. 1991).

One can expect that a species is either able to cope with soil hypoxia, or is selected against, as Huber et al. (2009) show for genotypes of *Trifolium repens*. Also new colonizers with a tolerance for coping with soil hypoxia can be expected to have a selective advantage. Indeed, we find a divergence in species composition between treatments as the floristic dissimilarity increases over time. This is more pronounced on the organic soil and mainly caused by a divergent shift in species abundance between treatments and less due to species turn-over. This is in contrast to previous studies which reported no strong evidence that mowing with heavy machines results in an other vegetation composition than traditional hand-mowing (Huhta et al. 2001; Liira et al. 2009). Our results indicate that this can be explained by the variation in sensitivity of soils to compaction.

So, machine mowing on organic soils can aggravate waterlogging effects and thereby affect plant performance. Consequently, this leads to an advantage to species that can cope with periodic hypoxia, and thus to changes in the vegetation.

Explaining treatment effects by differences in traits

Along with the increasing floristic dissimilarity, we also found differences in plant traits between treatments when evaluating community traits based on species presence-absence data and species abundance data. In the literature, monitoring the aboveground plant traits is the prevailing method of evaluating plant community responses to environmental gradients

(Lavorel et al. 2008). However, a priori, we only expected a treatment effect on belowground traits.

We found a strong increase in abundance of species with superficial root growth in the machine mown treatment on organic soil and a decrease in species that are less tolerant to hypoxia. This was also reflected in the relatively high root biomass in the upper 10 cm of the soil layer in the machine mown treatment in the organic soil.

Contrary to our hypothesis, we found no increase in cover of plant species that produce at least 15 % aerenchyma in the machine mown treatment, even though we found differences in redox potential between the treatments (Eh<330 mV in organic soils suggests hypoxic conditions). We have two possible explanations for this effect. The first is that, while on the one hand, soil aerenchyma formation is a good strategy to cope with soil hypoxia (Vartapetian and Jackson 1997), on the other hand production of aerenchyma may be restricted by the physical pressure in compacted soils (Engelaar et al. 1993; Striker et al. 2007). This may put constraints on the spread of aerenchyma-forming species and provide an explanation for the lack of dominance of aerenchyma-forming species. The second explanation is that the higher amount of aerenchyma is not readily expected in organic-sandy soils with redox values not low enough to form toxic compounds for the roots (Laanbroek 1990; Ponnamperuma 1984). These effects may be more pronounced in compacted moist soils with higher clay content (Rasiah and Kay 1998).

Coinciding with the increasing floristic dissimilarity, we found a consistent treatment effect on the commonly used aboveground trait canopy height, but not on leaf traits (SLA and LDMC). We suggest that the reaction of aboveground maximum canopy height in response to machine mowing on organic soil could be related to the changing belowground conditions. Canopy height and rooting depth have been mentioned as highly correlated traits (Douma et al. 2011). Therefore, we argue that a lower canopy height could be an indirect effect of rooting depth, imposed by the increase of superficially rooting species. The main effect of year on community SLA in both fields can be explained by the decrease in nutrient availability due to the cessation of fertilization (Wright et al. 2001).

The response of root growth strategies to the different mowing treatments is in agreement with an effect on the Ellenberg-moisture values in the different mowing treatments. Machine mowing on the organic soil resulted in lower soil aeration, consequently leading to plant species communities with higher average Ellenberg-moisture values. On sandy soil, no clear effect of machine mowing on soil aeration was found. Consequently, we also found no treatment effect on Ellenberg-moisture values on this soil type. This thus shows that the species replacement in the machine mown treatment on the organic soil is directed towards the wetter end of the spectrum (Ellenberg et al. 1992). The results from the Ellenberg-nitrogen values suggest that the removal of nutrients via mowing on organic soil could be more effective than on sandy soil, but we found no indication that the differences in mowing treatment had any effect on this.

Irrespective of above and below ground trait differences, the machine mown treatment seems to be slightly more species rich in both fields. We see two factors that might have led to these differences in diversity: i) dispersal. The dispersal vector, in this case the mowing machine, can be an important dispersal vector in the study area (Strykstra et al. 1997). ii) the species pool. The surrounding grasslands are managed the same way as the machine mown plots; the species of the species pool might therefore fit better into the machine mown plots.

In conclusion, species-rich grasslands on organic soil, but not on sandy soil, can be expected to diverge from historical grassland communities which were traditionally hand mown. We suggest that this happens in response to changing soil physical conditions induced by soil compacting machine mowing. As a result of the altered belowground growing conditions, we found shifts in community belowground traits. This may be, as in the case of canopy height, reflected in the aboveground traits. It thus emphasizes the need for evaluation of both aboveground and belowground plant traits when belowground plant organs are expected to respond to the studied environmental gradient. From the perspective of nature conservation, the impact of heavy machines may not necessarily lead to an undesired and less valuable plant species community. On the contrary, as in the case of our study site, many valuable yet different plant species can be found in both treatments.

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References

Armstrong W, Justin S, Beckett PM, Lythe S (1991) Root adaptation to soil waterlogging. Aquat Bot 39:57–73

Baayen RH (2011) languageR: data sets and functions with "Analyzing linguistic data: a practical introduction to statistics". R package version 1.2

Bailey-Serres J, Voesenek LACJ (2008) Flooding stress: acclimations and genetic diversity. Annu Rev Plant Biol 59:313–339

Bakker JP (1989) Nature management by grazing and cutting, vol 14. Kluwer Academic Publishers, Dordrecht

Bakker JP, Elzinga JA, de Vries Y (2002) Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils. Appl Veg Sci 5:107–120

Bates D (2011) Linear mixed model implementation in lme4. Available at: http://cran.r-project.org/web/packages/lme4/vignettes/Implementation.pdf

Bates D, Maechler M, Bolker B (2011) lme4: linear mixed-effects models using S4 classes. R package version 0999375-39

Bignal EM, McCracken DI (1996) Low-intensity farming systems in the conservation of the countryside. J Appl Ecol 33:413–424

Borchert H, Graf R (1988) Zum Vergleich von Penetrometermessungen, durchgeführt bei unterschiedlichem Wassergehalt. Z Pflanzen Bodenk 151:69–71

Colmer TD (2003) Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. Plant Cell Environ 26:17–36

De Willigen P, Van Noordwijk M (1989) Model-calculation on the relative importance of internal longitudinal diffusion for aeration of roots of non-wetland plants. Plant Soil 113:111–119

Dierschke H, Wittig B (1991) Die Vegetation des Holtumer Moores (Nordwest-Deutschland). Veränderungen in 25 Jahren (1963–1988). Tuexenia 11:171–190

Douma JC, Aerts R, Witte JPM, Bekker RM, Kunzmann D, Metselaar K, van Bodegom PM (2011) A combination of functionally different plant traits provides a means to quantitatively predict a broad range of species assemblages in NW Europe. Ecography 35:294–305

Ellenberg H, Weber HE, Paulissen D, Werner W, Düll R (1992) Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18:1–248

Elzenga JTM, van Veen H (2010) Waterlogging and plant nutrient uptake. In: Mancuso S, Shabala S (eds) Waterlogging, signalling and tolerance in plants. Springer-Verlag Berlin, Heidelberg

Engelaar WMGH, Van Bruggen MW, Van Den Hoek WPM, Huyser MAH, Blom CWPM (1993) Root porosities and radial oxygen losses of rumex and plantago species as influenced by soil pore diameter and soil aeration. New Phytol 125:565–574

Fuller RM (1987) The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930–1984. Biol Conserv 40:281–300

Gaudet CL, Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. Nature 334:242–243

Gerrard J (1982) The use of hand-operated soil penetrometers. Area 14:227–234

Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer Associates Inc., Sunderland

Hamza MA, Anderson WK (2005) Soil compaction in cropping systems—a review of the nature, causes and possible solutions. Soil Tillage Res 82:121–145

Henle K, Alard D, Clitherow J, Cobb P, Firbank L, Kull T, McCracken D, Moritz RFA, Niemela J, Rebane M, Wascher D, Watt A, Young J (2008) Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe—a review. Agric Ecosyst Environ 124:60–71

Hoagland DR, Arnon DI (1950) The water-culture method for growing plants without soil. Circ. 347. Univ. of Calif. Agric. Station, Berkeley

Hooftman DAP, Bullock JM (2012) Mapping to inform conservation: a case study of changes in semi-natural habitats and their connectivity over 70 years. Biol Conserv 145:30–38

Huber H, Jacobs E, Visser EJW (2009) Variation in flooding-induced morphological traits in natural populations of white clover (Trifolium repens) and their effects on plant performance during soil flooding. Ann Bot 103:377–386

Huhta AP, Rautio P, Tuomi J, Laine K (2001) Restorative mowing on an abandoned semi-natural meadow: short-term and predicted long-term effects. J Veg Sci 12:677–686

Jackson MB, Armstrong W (1999) Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. Plant Biol 1:274–287

Jafarzadeh F (2006) Dynamic compaction method in physical model tests. Scientia Iranica 13:187–192

Jensen LS, McQueen DJ, Shepherd TG (1996) Effects of soil compaction on N-mineralization and microbial-C and -N.1. Field measurements. Soil Tillage Res 38:175–188

Justin SHFW, Armstrong W (1987) The anatomical characteristics of roots and plant response to soil flooding. New Phytol 106:465–495

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, van Groenendael JM, Klimes L, Klimesova J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje G, Bossuyt B, Dannemann A, Endels P, Gotzenberger L, Hodgson JG, Jackel AK, Kuhn I, Kunzmann D, Ozinga WA, Romermann C, Stadler M, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Cornelissen JHC, Eriksson O, Garnier E, Peco B (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. J Ecol 96:1266–1274

Knevel IC, Bekker RM, Bakker JP, Kleyer M (2003) Life-history traits of the northwest European flora: the LEDA database. J Veg Sci 14:611–614

Laanbroek HJ (1990) Bacterial cycling of minerals that affect plant growth in waterlogged soils—a review. Aquat Bot 38:109–125

Laughlin DC, Leppert JJ, Moore MM, Sieg CH (2010) A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. Funct Ecol 24:493–501

Lavorel S, Grigulis K, McIntyre S, Williams NSG, Garden D, Dorrough J, Berman S, Quetier F, Thebault A, Bonis A (2008) Assessing functional diversity in the field—methodology matters! Funct Ecol 22:134–147

Lehsten V (2005) Functional analysis and modelling of vegetation—plant functional types in a mesocosmos experiment and a mechanistic model. University of Oldenburg, Oldenburg

Liira J, Issak M, Jogar U, Mandoja M, Zobel M (2009) Restoration management of a floodplain meadow and its cost-effectiveness—the results of a 6-year experiment. Ann Bot Fenn 46:397–408

Londo G (1976) Decimal scale for releves of permanent quadrats. Vegetatio 33:61–64

Nevens F, Reheul D (2003) The consequences of wheel-induced soil compaction and subsoiling for silage maize on a sandy loam soil in Belgium. Soil Tillage Res 70:175–184

Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MHH, Wagner H (2008) Vegan: community ecology package. R package version 115-1 Available at: http://cranr-projectorg/, http://veganr-forger-projectorg/

Ponnamperuma FN (1984) Effect of flooding on soils. In: Koalowski TT (ed) Flooding and plant growth. Academic, New York, pp 9–45

Quested H, Eriksson O, Fortunel C, Garnier E (2007) Plant traits relate to whole-community litter quality and decomposition following land use change. Funct Ecol 21:1016–1026

Rasiah V, Kay BD (1998) Legume N mineralization: effect of aeration and size distribution of water-filled pores. Soil Biol Biochem 30:89–96

RDCT (2008) R: a language and environment for statistical computing

Ryser P, Urbas P (2000) Ecological significance of leaf life span among Central European grass species. Oikos 91:41–50

Shipley B (2006) Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. Funct Ecol 20:565–574

Soane BD, Dickson JW, Cambell DJ (1982) Compaction by agricultural vehicles: a review. Soil Tillage Res 2:2–36

Striker GG, Insausti P, Grimoldi AA, Vega AS (2007) Trade-off between root porosity and mechanical strength in species with different types of aerenchyma. Plant Cell Environ 30:580–589

Strykstra RJ, Verweij GL, Bakker JP (1997) Seed dispersal by mowing machinery in a Dutch brook valley system. Acta Botanica Neerlandica 46:387–401

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press

van Bochove E, Beauchemin S, Theriault G (2002) Continuous multiple measurement of soil redox potential using platinum microelectrodes. Soil Sci Soc Am J 66:1813–1820

Van Straalen NM, Rijninks PC (1982) The efficiency of Tullgren apparatus with respect to interpreting seasonal-changes in age structure of soil arthropod populations. Pedobiologia 24:197–209

Vartapetian BB, Jackson MB (1997) Plant adaptations to anaerobic stress. Ann Bot 79:3–20

Visser EJW, Bogemann GM (2003) Measurement of porosity in very small samples of plant tissue. Plant Soil 253:81–90

von Kutschera L, Lichtenegger E, Sobotik M (1982) Wurzelatlas mitteleuropaischer Grundlandpflanzen. G. Fischer Verlag, New York

Voorhees WB, Evans SD, Warnes DD (1985) Effect of preplant wheel traffic on soil compaction, water use, and growth of spring wheat. Soil Sci Soc Am J 49:215–220

Walker KJ, Stevens PA, Stevens DP, Mountford JO, Manchester SJ, Pywell RF (2004) The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biol Conserv 119:1–18

Wallin L, Svensson BM, Lonn M (2009) Artificial dispersal as a restoration tool in meadows: sowing or planting? Restor Ecol 17:270–279

Weiher E, van der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O (1999) Challenging theophrastus: a common core list of plant traits for functional ecology. J Veg Sci 10:609–620

Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. Trends Ecol Evol 21:261–268

Wiengweera A, Greenway H, Thomson CJ (1997) The use of agar nutrient solution to simulate lack of convection in waterlogged soils. Ann Bot 80:115–123

Wilson PJ, Thompson K, Hodgson JG (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. New Phytol 143:155–162

Wright IJ, Reich PB, Westoby M (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. Funct Ecol 15:423–434

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827